THE PROTECTIVE VALUE OF ACTION, VOLI-TIONAL OR OTHERWISE, IN "PROTECTIVE MIMICRY."*

By F. M. Webster.

Whatever in the form, color or actions of an organism tends to enable it to escape from its enemies, or more readily secure a proper supply of food, is, to a certain extent, protective in its effects. Forms, not in possession of such advantages, will, in case of an unusual abundance of enemies, or a deficit in the supply of food, be the least likely to survive. In this paper it is the intention of the author to discuss only such cases of "protective mimicry" as require some special movements, or the assumption of some peculiar or unique position, on the part of the protected form, in order to continue or complete the deceptive effects of its shape, color or coloration.

There are a number of insects that, prepared and placed in our cabinets, have comparatively little resemblance to each other, while in the midst of life and activity, are distinguishable from each other only with extreme difficulty. An example may be found in *Podosesia syringæ* Harr., which somewhat resembles *Polistes annularis* Fabr., in form, while its movements are almost an exact reproduction of those of the latter species, which is an armed wasp, while the former is a helpless moth. The Varying Hare, *Lepus americanus virginianus* Harlan, no doubt derives more or less protection from the color of its fur, but this protection does not appear to be supplemented by any correlative action on the part of the animal itself.

Many naturalists object to the use of the term "protective mimicry," for the reason that it implies mental capabilities supposed to be confined to the human race. The statement is made, and by those whose opinion is worthy of the greatest respect and most careful consideration, that the influences of natural selection are amply sufficient to account for all such phenomena, and that we do not need to assume the presence of volition as a factor in such phenomena. In some quarters the initial step, in an investigation of the phenomenon of "protective mimicry," is to close the door, so to speak, against any possibility of the most primitive kind of intelligence, on the part of the mimicing species, while to admit that a mimicing insect has any conception of its own appearance, is the most dangerous sort of heresy. Now there are

^{*} Read before the Ohio State Academy of Science, December 30, 1896.

quite a large number of zoölogists who both work and think, who do not believe that natural selection is adequate to explain all of the phenomena that come to the notice of the naturalist, and as a leader of those who hold this view, we have that venerable thinker, Herbert Spencer. It is clear enough that natural selection will maintain or even perfect what has already been begun, but that it can set the machinery of protective mimicry in motion—can bring a case of protective mimicry or coloration into existence, seems extremely doubtful. In the first place, we must remember that "self-preservation is the first law of nature," even in man. No human being will voluntarily take his or her own life unless mentally deranged, or as a sacrifice to some great and important principle, or to save the lives of others. Old and battle-tried soldiers, whose acts of bravery have become known from one side of the world to the other, have acknowledged that the impulse to break and run, when first going into battle, had each time to be overcome. If selfpreservation is the first law of nature, then fear and the sense of pain are the police powers, so to speak, that enforce the law. The soldier who drops his gun and runs away, instead of facing the enemy, has allowed the fear of pain or death to overcome his sense of duty and he seeks a place of greater safety; seeks to preserve his life. Among all animal life below man, we find a different condition to exist, in that the whole aim and object of life is to reproduce. The same phenomena may be observed, even among plants, the whole of the remaining vitality of an injured tree or a girdled vine, being exhausted in producing a few seeds or seed inclosing fruit. In fact, almost a parallel may be observed to some extent among consumptive men and women. Among lower animal life, unless the young require the protecting care of the parents, as soon as this duty of reproduction is accomplished death, generally speaking, occurs, although among insects the period of reproduction may vary from a few hours to several years, according to species. Protection, in the egg stage, is usually accomplished, where such is needed, by the mother insect in her selection of a place of oviposition, but both herself and the larvæ may need protection from natural enemies, and such protection may result from a close resemblance to other protected species, or to inanimate objects, thus deceiving, to a greater or less extent, the natural enemies that threaten their destruction. It often occurs that the form and color of the adult or of the larva is such as to afford protection, but there are many cases, where, without the assuming of certain positions, to represent forms not preyed upon, or inanimate objects, like twigs, lichens or portions of flowers, or where peculiar movements are

necessary to complete the deception, form and color would fall far short of protecting. The point in dispute is as to whether these actions are of volition, and with the anticipation of protection to be derived therefrom, or are they involuntarily, and to be classed with the blushing of a timid maiden when becoming suddenly confused, or the whitening of the face of the less timid, when brought suddenly face to face with what appears certain death? The timid maiden is in no danger, and blushes not because she intended or wished to, but because she had no power to avoid so doing; while the frightened one was in danger, but equally unable to prevent a different change of color in her face, though no protection would result. If, as we suppose, the sense of pain decreases, as we descend in the scale of animal life, than the action that, with form and coloration, tend to deceive the enemy, must be made in order to escape destruction. A recent writer in Natural Science (Vol. IX, p. 299) states that while sitting in a tree, rifle in hand, waiting for a tiger, his attention was caught by a kind of slow cricket, which exactly resembled a small patch of gray lichen, skurrying round the trunk of a neighboring tree, with a lizard in full pursuit. "Just as the lizard came up with it, the cricket, falling in with a slight depression in the bark, stopped dead and flattened itself out, and the lizard was utterly confounded. There it stood, looking ludicrously puzzled at the mysterious disappearance of its prey, which was just under its nose." Here we have a sense of danger, a fear of death, and an attempt to escape death by flight; and when still pursued, certain actions that rendered the peculiar coloration of the insect of greater life-saving value than flight, were employed. With no knowledge of its own resemblance to a patch of lichens, and equally ignorant of the protective value of this resemblance, would the insect not have continued to attempt escape by further flight? How did it know that the pursuer was an enemy? How did it become aware that, to receive the benefit of its appearance, it must stop, when it had before followed the opposite course? If it had no knowledge of its appearance, how would it be able to separate one of the opposite sex from a patch of lichen? Without such a knowledge how can there be sexual selection at all?

Under the head of "A Case of Mimicry," Prof. Otto Lugger, in Entomological News, Vol. VI, pp. 138-140, gives a quite similar case of protective mimicry, as observed by him in *Marmopteryx gibbicostata* Walk. Professor Lugger saw on an elm tree what appeared to be the remains of a moth that had apparently been left over from the dinner of a spider, and, recognizing it as new to his collection, like every

other entomologist, preferring a poor specimen to none, attempted to secure it, when he was astonished to see his treasure take wing and disappear. Returning again to the same tree an hour later, he observed a second specimen, or perhaps the same one in the same position, but this took wing and disappeared. Returning again next day, he began to brush the trunk of the tree with a small limb, as is usually done in flushing Catocala. Finally, a moth alighted within two feet of him, ran rapidly a few inches and disappeared. It was then that the observer saw that the moth, after reaching the tree, would run to some projecting piece of bark that had a certain gray color so common upon old elm trees, then make a quarter turn, and fold its wings in a peculiar way upon the spot selected, that blended so well with it as to become invisible. In the normal position of these moths when at rest the color of the upper surface of the wings would contract with the color of the surface on which it was resting; as only the color and markings of the under side of the lower wing, and a narrow margin of the upper edge of the under side of upper wing, harmonize with the grayish spots before mentioned, and therefore these last must be displayed and the others hidden. The moth by making a quarter turn, and by pushing the upper wings deeply between the lower ones, effectually hides all colors not in harmony with its surroundings. As the colors upon the exposed parts vary somewhat from a very pale to dark, the insect, in order to render the deception complete, must select a spot of the proper shade to correspond; yet Prof. Lugger states that of the hundreds of moths he saw, none could be detected upon the trees unless the spot upon which they were observed to settle was kept carefully in sight until they were approached closely. In this case the deception was more largely a matter of action than of coloration, and the action would certainly imply a knowledge of not only the colors of its own wings but of its surroundings also. Collectors of Catocala are familiar with similar phenomena among that group of moths, as a scar or slight blaze, such as is often made by woodmen to mark paths or boundaries, are more often selected for resting places than other parts of the trees.

In North American Entomologist, Vol. I, p. 30, Dr. D. S. Kellicott has called attention to the fact that the moth *Alaria florida* Guen., conceals itself during the day in the withering blossoms of the Evening Primrose, *Œnothera biennis*. The inner two-thirds of the fore wings of this moth are bright pink, while the outer third, hind wings and abdomen, are pale yellow. The moth enters the flower before day,

with its body resting upon the style, the four-parted stigma projecting beyond the tip of the abdomen, appearing like a part thereof, and when the sun appears the two petals that were above the moth soon wilt and fall down over the roof-like wings, concealing the hinder portion, leaving the yellow part exposed as a part of the blossom, and so effectually is the moth concealed in this way during the day, that only a trained eye can detect its presence, and even then with extreme difficulty.

Some time after Dr. Kellicott had published his observations, and before I knew of them, I find, from looking over some old note books where I had recorded observations made in Illinois, that a specimen of this moth was taken by myself under much the same circumstances, except in this case the pink color was exposed from under a reddening, discolored leaf of Evening Primrose, in such a manner that the *yellow* was concealed and the deception was so marked that I made a record of it at the time. I still have the moth in my possession, and I have never taken a specimen except on this plant, and concealed in the manner indicated by the observations of Dr. Kellicott and myself.

In "A Naturalist in the Transvaal," pp. 41, 42, Mr. W. L. Distant-calls attention to the fact that while a butterfly, *Hamanumida dædalus*, in Senegambia, Calabar and the Cameroons, according to report, always settles with the wings vertically closed, and which so closely resemble the soil of the district, that it can with difficulty be seen, the color varies with the soil in different localities, yet in the Transvaal, and Natal, he was never able to observe it to rest except with horizontally-expanded wings, by which its protection was almost equally insured, by the assimulative color of the same to the rocks and paths on which it was usually found. Here we have an insect breaking away, or at any rate differing radically from a prevailing habit, where such habit would tend to expose it to natural enemies, and following that habit where it derives protection therefrom.*

In the case of *Podosesia syringæ*, which when in flight the abdomen has almost the exact position of *Polistes annularis*, when it is at rest, the posterior segments are bent downward and kept in motion, and if

^{*}While quite foreign to this particular point, it is interesting to note the difference in the action of our domestic sheep, in different parts of the country, on the appearance of sudden danger, like a wolf or dog. In the eastern and central-western states, a flock will break and run for a place of safety, and if still followed will scatter, each individual for itself. But in the far West, on the appearance of a like danger, the sheep will run directly to a common centre, and arranging themselves in a circle, heads outward, await further movements of the enemy.

it falls to the ground it will walk about precisely like the wasp it seems to resemble the most closely, so that its actions constitute by far the greater portion of the mimicry, and therefore are to the greatest extent protective in effects.

Among those species which resemble ants the most closely, and appear to derive protection therefrom, we find that, besides a more or less close resemblance in form and color, they have the erratic, rapid movements of such species of ants as they most resemble. Pilophorus bifasciatus Fab., a species of Hemiptera which is here in Ohio frequently associated with a species of black ant that is common and very often observed running up and down the trunks of trees and out on the limbs and twigs, does not closely resemble one of these ants when pinned and placed in the cabinet of a collector; but when running about over the trees they have the quick, erratic movements of the ants, and are then very difficult to distinguish from their associates.* In this case the deception is largely due to movement, and but for this there would be little resemblance. Belt, in "The Naturalist in Nicaragua," p. 314, speaks of a species of spider that appeared so exactly like a species of stinging ant that he did not distinguish the difference until he had killed the spider, and adds that "the resemblance is greatly increased by the spider holding up its two fore legs, like antennæ, and moving them about just like an ant."

Not over a couple of hundred yards from where I am now standing I was some years ago collecting small insects from the leaves of an elm tree, and saw what at a glance I took to be the excreta of a bird on the upper surface of a leaf, and, avoiding it, was busily engaged with my collecting. On making a sudden thrust I brought my hand in direct contact with the leaf, and not perceiving any excreta on my hand looked for an explanation, when, to my utter astonishment, the larger portion of the supposed excreta was observed to take legs and run across the leaf, and I found that it was nothing more or less than a small spider, whose back was clouded with a blackish area, surrounded with white. A white splotch remaining on the leaf proved to be only an irregular sheet of spider web, but almost exactly counterfeiting the appearance of semiliquid bird excreta that had become dried, and I saw at once through the whole deception. Taken separately, the spider was easily recognized, but placed on its sheet of thin white web and the deception was

^{*}In this case the rays of light reflected from the polished, black surface of the abdomen of the ant, appear like a transverse whitish band, very like in appearance to the transverse white fasce on the wings of the bug.

complete, and I have no doubt but that it not only escaped its enemies, but secured a better supply of food in consequence of its concealment, though in plain light, in a most exposed position. Mr. Henry O. Forbes, in his "A Naturalist's Wanderings in the Eastern Archipelago," p. 63, gives a similar experience of his in Java. In this case the observer saw what he supposed to be a butterfly at rest on a splotch of bird excreta on a leaf. Mr. Forbes carefully approached his prize until he was able to seize it between his fingers, when, to his astonishment, the wings parted from the body, which was left behind, and he still thought it had adhered to a small splotch of bird excreta until he touched the latter with his finger to find if it was glutinous, when, to his delighted astonishment, he found that the supposed excreta was really a peculiarly colored spider lying on its back, with its feet crossed, and on an irregularly shaped film of web, appearing like a splotch of excreta, with its central and denser portion of a pure chalk like color, streaked here and there with black, the white margin being drawn out into a narrow streak, with a slight thickening at termination near the margin of the leaf. Two years after, in Sumatra, Mr. Forbes, while waiting for his servants to procure some botanical specimens for him, rather dreamily plucked what appeared to be an excreta-marked leaf, and, while looking at it, mentally wondered why it was that he had never found a second specimen of the curious spider found in Java, when suddenly the supposed excreta bit him, and he was astounded to learn that he actually had a second specimen in his hand (loc. cit., p. 216).

In transmitting his specimens to Rev. O. P. Cambridge, for determination, Mr. Forbes used this expression: "the similitude is so exact that the spider might have had consciousness, and it could not have been more exact if the spider did have it," referring, of course, to the placing of itself on its sheet of web and the deceptive resemblance previously mentioned, though he really had no intention of crediting the spider with any conscious design, as Rev. O. P. Cambridge at first supposed. The latter gentleman, however, offered the following explanation of the phenomenon (loc. cit., pp. 119-121): "It seems to me, on the contrary, that the whole is easily explained by the operation of natural selection, without supposing consciousness in the spider in any part of the process. The web on the surface of the leaf is evidently, so far as the spider has any design or consciousness in the matter, spun simply to secure itself in the proper position to await and seize its prey. The silk, which by its fineness, whiteness and close adhesion to the leaf causes it to resemble the more fluid parts of the excreta, would gradually attain

those qualities by natural selection, just as the spider itself would gradually, and probably pari passu, become, under the influence of the same law, and more and more like the solid portion." And further, in a foot note on p. 121: "Is not this exactness probably the result of the unconsciousness of the spider? Conscious-design would possibly have resulted in a failure and abandoning the plan, or at least in a more clumsy imitation."*

To a great many naturalists it would appear as though if consciousness were present at all it would first exhibit itself in protecting life and afterwards in sustaining it. Without life food would be unnecessary, and the same consciousness that would lead the spider to take certain precautions to sustain life would impel it to take other or, perhaps, the same precautions to protect its life. The earlier attempts might be crude, but so long as they obscured the spider from the equally crude vision of either foe or victim, it would suffice. Of course, if it should be found that these species of spiders are inedible, then the whole effect of the deception would be to aid in sustaining life, but this is yet to be shown. Besides, it does not appear impossible that a kind of obscure and limited consciousness may have developed, springing, perhaps, from inherited instincts sufficient to enable these spiders and various species of insects to take advantage of action or movements, in order to protect their lives and perpetuate their species, but not extending beyond this point in development.

When, in the earliest development of animal life on the globe, one form or individual began to prey upon another, then self-preservation became necessary, and death a catastrophe to be feared and avoided. We would, here, have the first fear-incited efforts put forth to escape destruction by flight—the first impulse that seizes even man at the present day, when suddenly exposed to impending danger. The next effort, usually put forth by an organism, is to hide or secrete itself from a danger that, perhaps, cannot be avoided by flight. The second of these efforts, it is possible, might have followed the first very rapidly in time of development, and, later on, as the struggle for life became more severe between different forms, concealment for the purpose of surprising and capturing prey might have developed, and still later, the attempt at defense on the part of the form pursued, would lead to trials of strength between the attacking organism and the organism attacked,

^{*}These isolated observations give us no data whereby to judge to what extent individual spiders vary from each other in their architecture, or to what extent, if any, the young profits by imitating its parents.

but the object of all of these efforts would be the protection of life, by escaping capture and securing food to sustain that life, and the most successful would be the most apt to survive.

But have we not had, during all of this time, a consciousness of possible destruction and volition in the efforts put forth to get out of the way of an enemy in pursuit? Do not these, in fact, coexist with animation itself; and does not their presence really afford natural selection the primary foundation with which to begin the development of certain characteristics, and perfect such to an extent necessary to the life of an organism?

Another kind of phenomena, commonly termed feigning death, also comes within the scope of this paper, and includes such species as, when they are alarmed, either fall to the ground or assume certain rigid positions while attached to plants, or both, so as to appear either dead or like some lifeless object. Many insects, when disturbed, will draw up their legs and falling down remain perfectly still and rigid until the supposed enemy has passed on. Very many of our beetles do this, and because of our common opossum Didelphys virginiana, taking a similar course in its attempts to escape death, the action has been vulgarly termed "playing possum." Species belonging to the Coleopterous genera Chlamys and Exema, however, are shaped and colored so as to almost exactly represent the excreta of caterpillars, and when feeding, if disturbed, will drop to the ground if not caught by the leaves of the plant upon which they are feeding, and as they lay perfectly still, may be unrecognized by even fairly good entomologists. But, even the peculiar form and color of these insects would fall far short of protecting them while feeding, as their position at that time is so entirely different from that under which the excreta of caterpillars is usually observed; but, when they loose their hold, and drop to the upper surface of a lower leaf and either remain there or roll off and fall upon the ground, the deception is complete.

The resemblance of the larvæ of Geometridæ, to small twigs of trees and shrubs is everywhere observed, and as universally excites feelings of delight and surprise. When disturbed, the caterpillars assume a rigid position, more or less transverse to the limb upon which they are located, so that their position, together with the peculiar form and color of their bodies, render them not easily detected. In some species, the form of the body is such as to closely resemble a dead twig, even to the buds thereon. In this case it requires the assumption of the peculiar and rigid position, in order to complete the deception so far as it is

complete. On one occasion I found several eggs of a parasitic fly, one of the Tachinæ, placed among the bases of the legs, where the enemy could by no possibility have placed them had the caterpillar not occupied the peculiar position that it assumes when disturbed, thus showing that the deception was not complete.

An interesting point is here brought out, as, if all individuals attacked died, there would be no progeny and, therefore, no transmission of acquired life preserving consciousness, this could only be brought about by individuals that were attacked and escaped death. A new enemy would be more crude and bungling in its work, and thus allow of a greater number of escapes.

Now, in all of these phenomena we have form and color, supplemented by action, the object of all of which, taken together, is the protection Indeed, what else have these organisms to protect? And of what service would life be to an organism, without intelligence enough, to, in a measure, enable the possessor thereof to protect that life? all of these actions and movements, do we not have the same kind of consciousness, intelligence and volition, that we do in the case of a bird building a nest, with the expectations of laying its eggs in that nest and rearing its young? Are not all of these positions assumed, and movements made, with the sole aim of protecting life—continuing to live? Did not life and a life protecting intelligence co-exist, in the beginning. in some primitive organism, and was not this primitive, live-protecting intelligence, developed side by side with form and color, until the present conditions of affairs has been the result? The term "protective mimicry," is misapplied when used to designate this developed condition, because that term implies the personation of different objects, by different individuals of the same species, at the same time and in the same exact locality, which is not the case. But, though the same species may "mimic" different species in different localities, or different sexes may "mimic" different species, or one sex "mimic" and another not, yet these conditions cannot be changed to meet any sudden change of environment. Not only will the forms, colors and colorations continue long after the enemy to be protected from has disappeared, but as Mr. Distant has shown ("A Naturalist in the Transvaal," p. 66,) the "mimicing" form may continue to "mimic," even when the mimiced form has fallen far below it in point of numbers and becomes almost or even quite extinct.

It was Mr. Bates who wrote in his "The Naturalist on the Amazon," that "on the wing of the butterfly is written, as on a tablet, the story

of the modification of the species, so truly do all changes register themselves thereon," and it seems to me that in the brains of so-called "mimicing" species of insects, we might, if we could but understand the full significance of brain cells, read therein the records of the development of a dim, obscure consciousness, a volition and an intelligence that has kept pace with the requirements of these organisms, in protecting their lives and perpetuating their race. Man himself comes into the world, little less than a mere automaton, but with an inherited basis for future development of an individual consciousness. He begins his education with the alphabet, but does not transmit even a knowledge of this alphabet to his offspring, who must begin precisely where he himself began. But there has descended to his children, that which will enable them to master the alphabet with more aptitude and less difficulty. Now, if we descend the line of animal life, until we reach these insects whose movements go far toward perfecting the protection afforded by their form, color and coloration, may we not expect to find the foundation for a "species consciousness" that will enable the possessors to protect their lives from enemies of long standing and gradually, though, perhaps very slowly, adapt themselves to shunning the attacks of more recent foes? Or, to put the question in other words, with a protective appearance, will there not go either a consciousness of that appearance, or an inherited foundation for such a consciousness, that will the better enable an insect to apply its protective inheritance, and in the use of all of these, as a means of perpetuating its kind, follow strictly in the line of all other animal life?

NOTES ON THE TRANSFORMATIONS OF THE HIGHER HYMENOPTERA. II.

By A. S. PACKARD.

Polistes (probably P. canadensis Linn.).

Larva.—It differs generically from Vespa in its head being about twice as large; the body is much shorter, a third shorter than in Vespa, and more ovoid; the end sharper, the body narrowing rapidly towards the tip, which is more pointed than usual; towards the head it tapers rapidly, the prothoracic segment being small in proportion to the head. The lateral ridge of the body is but slightly prominent. The body is not entirely cylindrical, but very convex above, and flattened beneath. The last sternite is twice as broad as long; the sides of the anal opening